How much city is too much city? Biodiversity and ecosystem functioning along an urban gradient

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24 **Summary**

25 **1.** Over half of the world's population resides in urban areas, a huge proportion of which

26 occur along the coast. As cities expand, the ability of coastal ecosystems to provide the

27 services people need from them is in question. While it is well understood that coastal

28 development changes ecosystems, a quantitative understanding of such relationships

29 across the land-sea boundary is generally lacking.

30 **2.** We investigated how land cover—a potential indicator of stressors such as toxic

31 contaminants, nutrient loads, and extractive uses—related to empirically measured

32 ecosystem properties in freshwater (stream) and marine (intertidal) habitats in the Puget

33 Sound region of WA, USA. Specifically, we estimated how biodiversity

34 (macroinvertebrate family density and Simpson diversity), benthic net primary

35 productivity, and decomposition varied across six pairs of more and less urbanized,

36 coastal watersheds.

37 **3.** While freshwater biodiversity and marine primary productivity were significantly

38 lower in more urbanized watersheds, marine biodiversity, freshwater primary

39 productivity, and freshwater and marine decomposition rates were not significantly

40 different among watershed pairs.

41 **4.** Some watershed pairs differed more in the extent of urbanization than others, and

42 greater differences in imperviousness between watershed pairs were associated with

43 greater reductions in stream biodiversity in more urbanized watersheds. In contrast and

44 surprisingly, however, watershed pairs that were most different in imperviousness tended

45 to be least different in marine biodiversity.

46   **5.** We found no evidence that associations between biodiversity, ecosystem functions,

47   and urbanization attenuated from freshwater to marine habitats, as might be expected if

48   the land-sea boundary diminished effects of terrestrial development.

49   **6.** *Synthesis and applications.* These results add support to growing evidence that a

50   dichotomy between urbanized and non-urbanized ecological communities may be less

51   straightforward than is often assumed, and reinforce the idea that true ecosystem-level

52   management requires integrated land-sea planning. Thus, our study suggests that

53   conservation attention focused singularly on remote and relatively untouched places is

54   necessary but not sufficient in the Anthropocene. Similarly, this work implies that

55   jurisdictionally convenient but ecologically unjustified attention to terrestrial, freshwater,

56   or marine systems in isolation cannot be considered true ecosystem-based management.

57
58   **Key-words:** land-sea, ecosystem structure, ecosystem function, biodiversity, urban
59   gradient
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62
63   **Introduction**

64   Despite comprising ~2% of the global land surface, urban areas are home to more

65   than half of the world's population (UN 2014). In the US, 30-50% of people live in

66   coastal counties, primarily in cities (Crossett *et al.* 2013). Coastal cities are experiencing

67   especially rapid change, with urban expansion directly drawing down natural resources,

68   consuming undeveloped and agricultural lands, and influencing biodiversity and

69   ecosystem functions (Bulleri & Chapman 2010, SCBD 2012). While it is well understood

70   that coastal development changes natural ecosystems, a quantitative understanding of the

71   relationship between development and ecosystem function is generally lacking (but see

72   McClelland *et al.* 1997, Koch *et al.* 2009).

73   A robust understanding of how urbanization alters ecosystems, and what

74   conservation value remains within urban areas, is timely. Coastal cities concentrate many

75   social benefits for people because they serve as cultural hubs and centers of commerce

76   and trade (Ernstson *et al.* 2010), and there is increasing appreciation that they are also

77   places that nature's benefits are most needed (Granek *et al.* 2010). For example, there is

78   growing demand for natural vegetation and structures that improve freshwater quality for

79   both consumption and recreational purposes (e.g., McIntyre *et al.* 2015), provide coastal

80   protection from storms and sea level rise (Koch *et al.* 2009, Arkema *et al.* 2013), and

81   serve as nursery habitat for fishery and protected species (Beck *et al.* 2001). Meeting this

82   demand will require a rigorous scientific understanding of how urban development

83   changes ecosystem structure and function relative to other local, regional, and global

84   influences (Halpern *et al.* 2009, Alvarez-Romero *et al.* 2011).

85   The literature is replete with hypotheses about processes associated with urban

86   land development that modify ecosystem structure and function (Table 1). These

87   processes include increases in: species introductions, nutrient inputs, stream flow,

88   sediment runoff, water temperature, low-oxygen areas, toxic contaminants, and extractive

89   use. Often these hypotheses imply, directly or indirectly, that the effects of development

90   should be strongest on land, and attenuate but not necessarily extinguish in coastal marine

91   ecosystems (Alvarez-Romero *et al.* 2011). In some cases, it is clear that the influence of

92   terrestrial inputs, such as dissolved organic carbon, are diminished in aquatic systems, but

93   such findings remain a contentious area of investigation (Brett *et al.* 2009). Quantitative

94   evidence for specific urban impacts on ecosystem structure and function is beginning to

95   emerge (Cuffney *et al.* 2010), though few published studies consider the extent to which

96   urbanization effects are linked across land-sea boundaries (Stoms *et al.* 2005, Alberti *et*

97   *al.* 2007, Tallis *et al.* 2008, Beger *et al.* 2010).

98   Here, we test the hypothesis that ecosystem structure and function (hereafter,

99   ecosystem properties) of freshwater and nearshore marine habitats are strongly associated

100   with the extent of adjacent urbanization. We examine habitats in the region of Puget

101   Sound, WA, USA, an area of burgeoning population growth (PSRC 2015) with strong

102   land-sea connections. We investigate whether two measures of biodiversity and two types

103   of ecosystem functions in freshwater and marine habitats: (i) differ systematically

104   between more and less urbanized areas, with the expectation that more urbanized areas

105   would exhibit lower diversity and ecosystem functioning; and (ii) display equally strong

106   associations with urbanization, anticipating that relationships with urban land use are

107   stronger in freshwater than marine habitats.

108

109   **Materials and Methods**

110   *Study region*

111   The Puget Sound region includes the lands and waters from the crests of the

112   Cascade and Olympic mountains to the marine waters as far south as Olympia, WA,

113   north to the San Juan Islands and west to the mouth of the Strait of Juan de Fuca

114   (Ruckelshaus and McClure 2007; Fig. 1). Puget Sound itself is typically divided into 7

115   oceanographic basins based on physical and chemical properties (Simenstad et al. 2011).

116   The region is characterized by a full range of coastal land cover, from undeveloped to

117   intensely developed including uninhabited wilderness areas, three national parks, and

118   densely populated cities (0-232 people km^{-2}, including the metropolitan hubs of Seattle

119   and Tacoma). These features make this coastal region an excellent test bed for

120   understanding how ecosystem properties change along an urban gradient.

121

122   *Characterizing variability in urbanization and ecosystem properties: defining the urban*

123   *gradient*

124   We quantified watershed scale patterns of urbanization in streams that flowed

125   directly into Puget Sound using ESRI ArcGIS software suite (v.10.1). We used an

126   existing river basin geospatial data layer (PSNERP 2010) to select watersheds that were

127   ≤1,000 ha, and contained ephemeral and perennial streams (USEPA & USGS 2005).

128   Using watersheds that met these criteria, we considered four different geospatial data

129   layers that captured alternative aspects of urbanization: imperviousness (i.e., surface

130   areas that reduce infiltration and increase runoff; Schueler *et al.* 2009), roadways

131   (OpenStreetMap 2012), land use and land cover (LULC, Fry *et al.* 2006), and shoreline

132   armoring (PSNERP 2010). For the continuous data layers (imperviousness and roadways)

133   we calculated area weighted mean values for each watershed. For the categorical data

134   layers (LULC, shoreline armoring), we calculated the proportion of each watershed that

135   was classified as developed as well as the proportion of the associated shoreline that was

136   armored.

137   To characterize the rural-to-urban gradient, we reduced the dimensionality of the

138   four land cover data layers using principal components analysis (PCA) in Primer v6. This

139   approach also reduced the likelihood of confounding the relationship between data layers

140   used to generate the urban gradient *a priori* and covariates used to explore correlations

141   with our response variables *post hoc* (Alberti 2008, Spirandelli 2014). Prior to the PCA,

142   we normalized the data layers to ensure that they were equally influential in describing

143   the urban gradient. The first two principal components (PC1 and PC2) explained 92% of

144   the among-watershed variation in the original four LULC data layers (Table S1; Fig. 1a).

145   Increasingly positive values of PC1 (74%) corresponded to more human-modified

146   watersheds (specifically, those with greater imperviousness, road, and developed land

147   cover). Increasingly positive values of PC2 (18%) corresponded primarily to increased

148   armoring, after accounting for effects of imperviousness.

149

150   *Characterizing variability in urbanization and ecosystem properties: study design*

151   In order to account for well-known spatial variability in both abiotic (e.g.,

152   salinity) and biotic (e.g., recruitment) factors (Dethier *et al.* 2012), we collected data from

153   six pairs of watersheds characterized by perennial streams, with similar drainage areas,

154 occurring at similar latitudes, within the same oceanographic basins (5 pairs within

155 Central Puget Sound, 1 pair in Hood Canal), and spanning a wide range of urbanization

156 across Puget Sound (Fig. 1b, Table S2). Each pair consisted of a more and less urbanized

157 watershed, such that more urbanized watersheds were defined as those that were more

158 anthropogenically-modified (i.e., higher PC1 and PC2 scores). Nested within each

159 watershed, we selected two study sites, one each in freshwater and nearshore marine

160 habitats. This paired-watershed study design allowed us to test for an association of

161 urbanization with ecosystem properties in freshwater and marine habitats, while

162 controlling for as many other factors as possible.

163   Our study focused on biodiversity and two types of ecosystem functions—net

164 primary productivity and decomposition. Changes in biodiversity are a primary concern

165 related to urbanization (Pickett *et al.* 1997, Aronson *et al.* 2014, Beninde *et al.* 2015,

166 Clark *et al.* 2015). We evaluated two measures of biodiversity, the number of benthic

167 macroinvertebrate families (family density), and the distribution of individuals among

168 these families (Simpson diversity). Benthic macroinvertebrates have long been

169 considered useful indicator species in both freshwater (Morley and Karr 2002) and

170 marine (Bilkovic *et al.* 2006) habitats because they are relatively sedentary and tend to

171 respond quickly to changes in local environmental conditions. Net primary productivity

172 and decomposition are two ecosystem functions thought to respond directly to

173 urbanization, via associated changes in abiotic factors such as light and flow, or indirectly

174 via changes in ecological communities (Table 1). These functions are fundamental to the

175 production of new biomass and cycling of energy in ecosystems (Vitousek 1986, Cebrián

176 and Lartigue 2004).

177

178 *Characterizing variability in urbanization and ecosystem properties: biodiversity*

179   In marine habitats, we collected epibenthic macroinvertebrates along an ~100 m

180 length of coastline at each of the study sites (n=3 samples site^{-1}). Collections occurred in

181 July 2012, 2013, and 2014 using a benthic sled (1 m x 1 m opening, 1 mm mesh), towed

182 over 10 m transects at each site (~-0.5m tidal elevation). We sampled the epibenthic

183 community occurring within eelgrass beds (except for 3 sites in which eelgrass did not

184 occur; Table S2), and samples were stored on ice in the field and transferred to ethanol

185 for preservation within 24 hours.

186   In freshwater habitats, we leveraged existing long-term data on stream

187 invertebrates around Puget Sound (Puget Sound Stream Benthos 2015). To ensure

188 temporal comparability between marine and freshwater habitats, we focused on stream

189 macroinvertebrate data collected by a variety of regional agencies and environmental

190 organizations between 2012-2013 in the South Central Basin of Puget Sound (for detailed

191 methods, see King County 2009). Our analyses relied on count data aggregated at the

192 family level to maximize the number of database entries we could use (n=37 watersheds

193 ≤1,000 ha with perennial streams flowing directly into Puget Sound) and to ensure

194 consistency with analysis of invertebrate data we collected from marine habitats. We

195 examined all possible pairings of more and less urbanized watersheds contained within

196 this database, where urbanization was defined using the PCA described above.

197   For both marine and freshwater habitats, we quantified the number of

198 macroinvertebrates in each taxonomic family (Table S3, S4), a resolution considered

199 sufficient for capturing spatial differences in species composition for this region (Dethier

200   and Schoch 2006, Morley and Karr 2002). We used the observed number of invertebrate

201   families to estimate family density (number of taxonomic families observed) and

202   Simpson diversity (a measure of evenness) from each sample (with the vegan package in

203   R v3.1; Oksanen et al. 2015, R Core Team 2014).

204

205   *Characterizing variability in urbanization and ecosystem properties: net primary*

206   *productivity*

207   We assayed benthic freshwater and marine net primary productivity by tracking algal

208   growth on pre-rinsed unglazed ceramic tiles (10cm x 10cm x 0.5cm deep; n = 10 site^{-1}) in

209   June-August 2012-2013. In marine habitats, we used plastic ties to attach tiles to the tops

210   of 1m long vertical PVC poles spaced evenly along an ~100m length of coastline (~-0.5m

211   tidal elevation). In the freshwater habitats, we placed tiles exclusively in riffles every 2-5

212   m along a 100-200m reach. Tiles were attached to hardware cloth using plastic ties, and

213   hardware cloth was attached to the streambed using rebar. We collected tiles from both

214   freshwater and marine habitats after 8-12 weeks to determine algal biomass accrual.

215   Algal growth in streams was exclusively micro-algal (e.g. benthic diatoms) while marine

216   production was dominated by macroalgae such as *Ulva* spp. Tiles were stored on ice in

217   the field and processed in the lab within 24 hours.

218   Prior to processing, we rinsed the tiles of sediments and removed macroinvertebrates

219   visible to the naked eye to minimize overestimation of algal organic matter. We scrubbed

220   algae from the top surface of each tile using a bristled brush and filtered water. For

221   marine tiles, algal scrapings were placed directly into aluminum weigh boats, dried at

222   60°C for ≥72 hours, weighed, ashed at 400°C for 2 hours, and reweighed (Hixon and

223   Brostoff 1996). For freshwater tiles, twenty percent of the resulting 500 mL slurry was

224   filtered onto a pre-ashed, pre-weighed 47-mm GF/F filter. These samples were dried at

225   60°C for 24 hours, weighed, ashed at 400°C for 2 hours, and reweighed (Steinman *et al.*

226   2007). For both freshwater and marine tiles, the ash-free dry mass (AFDM) was taken as

227   an estimate of the organic content of algae present on the tiles at the time of collection.

228   We divided this measure of organic content by the amount of time the tiles were

229   deployed to estimate rates of net primary productivity. (Preliminary investigation of tiles

230   collected after 14, 28, 60, 90, and 120 days during a separate 2012 study suggested a

231   linear rate of algal increase over time; Samhouri *et al. unpublished data*).

232

233   *Characterizing variability in urbanization and ecosystem properties: decomposition*

234   To track litter decomposition, we collected freshly fallen, dried maple leaves

235   (*Acer* spp; freshwater habitats) or rinsed, drift eelgrass (*Zostera marina*; marine habitats)

236   and deployed these materials in mesh litter bags at each site (n = 8, 10 g bags site^{-1}). In

237   the marine habitats, we used plastic ties to attach litter bags to the tops of 1m long

238   vertical PVC poles spaced evenly along an ~100m length of coastline in August 2013 (~-

239   0.5m tidal elevation). In the freshwater habitats, we placed the litter bags exclusively in

240   riffles every 2m -10m along a 100-200m reach in early November 2012 and 2013. Litter

241   bags were attached to rebar (embedded within the streams) using plastic ties. We

242   collected litter bags from both freshwater (1-2 months later) and marine (4-6 weeks later)

243   habitats to determine litter loss rates. Litter bags were stored on ice in the field and

244   processed in the lab within 24 hours.

245   Prior to processing, we rinsed the litter bags of sediments and removed

246   macroinvertebrates visible to the naked eye to minimize overestimation of remaining

247   organic matter. These pre-processed samples were transferred to aluminum weigh boats

248   and dried at 60°C to constant weight for 24-72 hours, weighed, ashed at 400°C for 2

249   hours, and reweighed (Bretherton *et al.* 2011, Nicastro *et al.* 2012). For both freshwater

250   and marine litter bags, the ash-free dry mass (AFDM) was taken as an estimate of the

251   organic content of litter remaining at the time of collection. Decomposition rates were

252   estimated as the difference between initial litter bag weights (10g) and organic content

253   remaining at the time of collection, divided by the number of days the litters bags were

254   deployed.

255

256   *Characterizing variability in urbanization and ecosystem properties: other environmental*

257   *characteristics*

258   We measured several other environmental characteristics that may be associated

259   with the ecosystem properties described above (Table 2 and Supporting Information). We

260   estimated an average for each of the environmental characteristics at all of our study

261   sites.

262

263   *Analyses: categorical comparisons between more and less urbanized watersheds*

264   Our primary hypothesis was that differences in four ecosystem properties (family

265   density, Simpson diversity, net primary productivity, and decomposition) in marine and

266   freshwater habitats would be associated with the extent of urbanization in the surrounding

267   watersheds. We analyzed our data in two ways. First, we considered categorical

268   differences in urbanization (more vs. less urbanized) between watershed pairs.

269   Specifically, we conducted a paired t-test for each of the ecosystem properties in each

270   habitat to evaluate the null hypothesis of no difference between more and less urbanized

271   watersheds.

272

273   *Analyses: comparisons of ecosystem properties along a continuum of urbanization*

274   Because urbanization scores for some watershed pairs differed more widely than

275   for others (Fig. 1b; e.g., compare Pair 3 with Pair 6), we also examined pairwise

276   differences in ecosystem properties within each watershed pair. Because imperviousness

277   loaded more strongly than any other data layer on PC1 (Table A1), we estimated the

278   disparity in urbanization as the difference in imperviousness between the more and less

279   urbanized watershed in each pair (hereafter, impervious distance). Similarly, to estimate

280   the disparity in ecosystem properties, we calculated the difference in the average value of

281   each property between the more and less urbanized watershed in each pair (hereafter,

282   ecosystem property distance). We used ANCOVA to test for an effect on ecosystem

283   property distance (e.g., Simpson diversity distance) of impervious distance (a linear

284   covariate) and year (a categorical factor), along with their interaction. We used post hoc

285   pooling procedures to sequentially remove non-significant interactions terms, beginning

286   with the highest order interactions (Winer *et al.* 1991). This analytical structure

287   accurately reflected the paired design of our study and thus provided the strongest

288   available test of the effects of changes in land cover, while accounting for other

289   covariates (both measured [Table 2] and unmeasured).

290   Because we used a larger data set of watersheds for freshwater invertebrates, we

291   employed a slightly different set of analyses for freshwater invertebrate family density

292   and Simpson diversity. Specifically, we examined all possible pairings of the 37

293   watersheds using Mantel's test. Mantel's test is a regression in which variables are

294   distance matrices summarizing all possible pairwise similarities among sample locations.

295   We used it to determine whether watershed pairs that were more dissimilar in

296   imperviousness were also more dissimilar in ecosystem properties. We converted

297   impervious distance to non-impervious distance for these analyses in order to avoid

298   excessive Type II error inherent to Mantel's test when the correlations between predictor

299   and dependent variables are expected to be negative (Legendre and Fortin 2010).

300

301   *Analyses: comparison of the strength of relationships between ecosystem properties and*

302   *urbanization in freshwater and marine habitats*

303   To test the hypothesis that urbanization was more strongly associated with

304   ecosystem properties within freshwater habitats than within marine habitats, we

305   compared the strength of the impervious distance effect for biodiversity, net primary

306   productivity, and decomposition across habitats. To ensure that effect sizes were

307   comparable while avoiding confounding effects of different sample sizes between

308   habitats, we standardized each habitat-specific dependent variable (by subtracting the

309   mean and dividing by 1 standard deviation), conducted a linear regression of it against

310   impervious distance to estimate the 'urbanization' coefficient, and compared this value

311   (and its 95% CI) across habitats.

312

313   **Results**

314   *Characterizing variability in urbanization, biodiversity, and ecosystem functions*

315   The watersheds in our study captured a large range of variation in urbanization,

316   spanning 1% to >40% imperviousness and 25% to 100% shoreline armoring. We also

317   found considerable variation in ecosystem properties across our study sites. In marine

318   habitats, invertebrate family density varied 6-fold (range: 3-18 families), Simpson

319   diversity ranged almost an order of magnitude (0.07-0.79), net primary productivity

320   varied by almost 2 orders of magnitude (2.76×10^{-4} – 1.97×10^{-2} g day^{-1}), and

321   decomposition rates varied from nil to -0.4 g day^{-1}. In freshwater habitats, invertebrate

322   family density varied almost 5-fold (range: 6-29 families), Simpson diversity varied >3-

323   fold (0.26-0.9), net primary productivity ranged almost a full order of magnitude (1.02 x

324   10^{-4} – 8.3×10^{-4} g day^{-1}), and decomposition rates spanned a 5-fold range (-0.04 to -0.22 g

325   day^{-1}). Together, the wide range of land cover and ecosystem properties we observed

326   facilitated a strong test for associations between urbanization and ecosystem properties.

327

328   *Categorical comparisons of ecosystem properties in more and less urbanized watersheds*

329   For five of the eight ecosystem properties we tracked, more urbanized watersheds

330   were no different than less urbanized watersheds (Fig. S1). However, marine net primary

331   productivity (Fig. S1c) and the two measures of freshwater biodiversity (Simpson

332   diversity and family density; Figs. S1ef) were significantly lower in more urbanized

333   watersheds. Almost all other environmental characteristics (Table 2) did not differ

334   between more and less urbanized watersheds (Fig. S2). (The single exception was our

335   detection of greater stream phosphate concentrations in less urbanized than more

336   urbanized watersheds).

337

338   *Comparisons of ecosystem properties along a continuum of urbanization*

339   Categorical comparisons of ecosystem properties in more and less urbanized

340   watersheds obscured the complexity of differences in urbanization among watershed

341   pairs (Fig. 1b). In watershed pairs that were similar in imperviousness (i.e., <20%

342   difference), more urbanized marine habitats tended to have higher family density than

343   their less urbanized counterparts (Fig. 2). Counter-intuitively, as the impervious distance

344   between watersheds within a pair grew large, differences in marine family density

345   became negligible (Fig. 2; $p = 0.01$). There was not an association between marine

346   Simpson diversity distance and impervious distance (Fig. 2; $p = 0.64$).

347   In freshwater habitats, both family density distance (Fig. 2; $p < 0.001$) and

348   Simpson diversity distance (Fig. 2; $p < 0.001$) exhibited a negative relationship with

349   impervious distance, such that more urbanized watersheds tended to have lower family

350   density and Simpson diversity than less urbanized watersheds.

351   There was no association between impervious distance and either of the two

352   ecosystem functions we tracked, net primary productivity and decomposition (Fig. 3; all

353     $p > 0.20$). In addition, the distances between other environmental characteristics (Table 2)

354   were not significantly associated with impervious distance in either freshwater or marine

355   habitats (Fig. S2).

356

357   *Moving from land to sea: comparison of the strength of relationships between ecosystem*

358   *properties and urbanization in freshwater and marine habitats*

359   The two measures of biodiversity we tracked were negatively associated with

360   impervious distance in marine and freshwater habitats. However, the strength of

361   associations between family density distance and impervious distance, and that between

362   Simpson diversity distance and impervious distance, were similar in both marine and

363   freshwater habitats (Fig. 4). Because neither net primary productivity distance nor

364   decomposition distance were significantly associated with impervious distance in

365   freshwater or marine habitats (i.e., the slopes of these regression lines were not

366   significantly different than zero; Fig. 3), we can also reject the hypothesis that

367   urbanization was significantly more associated with freshwater ecosystem functions than

368   marine ecosystem functions.

369

370   **Discussion**

371   As coastal cities expand, understanding their impacts on ecosystems is critically

372   dependent on scientific knowledge about how the effects of human activities translate

373   across terrestrial, freshwater, and marine habitats. Urbanized ecosystems generate a wide

374   range of services on which people depend, including protection from severe weather and

375   climate impacts, improved air and water quality, stress relief, and food production

376   (Niemela *et al.* 2011). However, it is often assumed that "ecology [with]in cities" is

377   impaired or diminished relative to without, causing urban areas to rely strongly on

378   unpeopled ecosystems in distant, rural, and undeveloped locations (Jansson 2013). Here

379   we found that urbanization was not associated with predictable changes in freshwater and

380   marine ecosystem functions (net primary productivity and decomposition) and two

381   different measures of biodiversity were not consistently higher in less urbanized than

382   more urbanized areas across freshwater and marine habitats. Where negative

383   relationships between our measures of biodiversity and increasing urban land cover did

384   exist, they were strong enough that they did not diminish between freshwater and marine

385   habitats. Thus, rather than suggesting that ecosystem functions are compromised,

386   biodiversity is uniformly lower, or marine habitats are less affected by land cover in

387   urban areas, these results suggest that discussion of ecology within cities and

388   expectations for the services they can provide require more nuanced consideration. This

389   conclusion adds to a growing literature which, when viewed collectively, implies that

390   urbanizations impacts may not be consistent, straightforward, or uniformly negative

391   (Table 1). Further, our findings provide at least three lessons—one hopeful, another

392   cautionary, and a third motivational—for coastal conservation and management.

393   First, our results provide some optimism in the face of the accelerating expansion

394   of coastal cities, as increasing urbanization was not consistently associated with

395   increasing impairment of two key ecosystem functions in either freshwater or marine

396   habitats (Fig. 3). These two functions, net primary productivity and decomposition, are

397   fundamental to "healthy and resilient" ecosystems (Christensen 1995, Elliott and

398   Quintino 2007, Samhouri *et al.* 2010) advocated in calls for widespread implementation

399   of EBM (McLeod & Leslie 2009). They underpin the production of consumer biomass

400   (including consumers that serve as human foods; Pauly and Christensen 1995, Brown et

401   al. 2004) and the efficient recycling of energy and nutrients, an archetypal regulating

402   service (MEA 2005). Our observations of variation in net primary productivity and

403   decomposition encourage increased scrutiny of the idea that urbanization undermines

404   EBM goals focused on the maintenance of ecosystem functions. Though beyond the

405   scope of our study, it seems likely that factors largely independent of urbanization (Fig.

406   S2)—such as the influence of light (net primary productivity) and turbulence

407   (decomposition)—contributed most to the wide range of spatial variability in ecosystem

408   properties we observed. We also recognize that ecosystem properties could respond to

409   urbanization at different spatial scales than those addressed here.

410   We also note that we investigated relationships between urbanization and

411   ecosystem properties in a developed country with strong government oversight and

412   enforcement of development and pollution regulations. A second optimistic conclusion of

413   our work would be that careful and effective governance may reduce the potential for

414   disparity in ecosystem properties across the urban gradient. We suspect that urbanization

415   effects would be stronger in locales with less regulatory oversight or enforcement.

416   The second lesson from this research relates to oft-stated conservation and

417   management goals that focus on broad terms such as biodiversity, ecosystem functions,

418   and resilience (McLeod & Leslie 2009). Our work tells a cautionary tale suggesting that

419   these terms can be unsatisfactorily coarse, making it difficult to discern which ecosystem

420   properties are of greatest concern. Alternative indicators for a single ecosystem property

421   can conflict, as we saw for the two measures of marine biodiversity in this study. Where

422   changes are detected, as in this study with observations of lower macroinvertebrate

423   family densities at more urbanized sites in both freshwater and marine habitats, clarity of

424   purpose for choosing a particular indicator will help to inform actionable strategies for

425   meeting conservation and management goals (Samhouri & Levin 2012).

426   In the Puget Sound region and beyond, it is increasingly common to observe

427 environmental policies that call for integrated land-sea planning and ecosystem-based

428 management that crosses traditional social-ecological boundaries (POC 2003, PSP 2008,

429 Alvarez-Romero *et al.* 2011, Samhouri & Levin 2012). The third lesson from this study

430 motivates a call for support of such initiatives, as we found that associations between

431 ecosystem properties and urbanization did not diminish in strength between freshwater

432 and marine habitats. This finding runs counter to others suggesting that allochthonous

433 inputs from land are not as important as internally generated drivers in nearshore marine

434 environments (Brett *et al.* 2009, Steinberg *et al*. *2010*), and echoes more widely accepted

435 understanding of major river influences on marine ecosystems (Diaz & Rosenberg 2008).

436 The main difference is that in our study, we tested connections within much smaller

437 watersheds, typically thought to be of minimal influence on coastal marine ecosystems

438 (Smith *et al.* 2003, Halpern *et al.* 2009). Therefore, prospects for management of

439 terrestrial, freshwater, or marine systems in isolation seem marginal, whereas integrated

440 land-sea planning such as that spearheaded in the Puget Sound region by the Puget Sound

441 Partnership offers greater promise.

442   In conclusion, rather than providing unequivocal evidence for the negative

443 impacts of urban landscapes on biodiversity and ecosystem functions, our study supports

444 growing evidence that a dichotomy between urbanized and non-urbanized ecological

445 communities is less straightforward than is often assumed (Table 1). For example, the

446 negative association between freshwater diversity and urbanization observed in this

447 study, and established previously (Morley and Karr 2002), was striking not so much for

448 its mean effect size (Fig. 4), but for the amount of unexplained variance around the trend

449   (Fig. 2). As touched on above, one interpretation of such variability is as evidence that

450   the long history of progressive, environmental restoration and recovery actions in the

451   Puget Sound region may be working, even though it is heavily developed. More broadly,

452   if this interpretation is correct, it lends credence to the idea that conservation attention

453   focused singularly on remote and relatively untouched places, and on land or at sea but

454   not at the interface between them, is necessary but not sufficient in the Anthropocene.

455

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464   **References**

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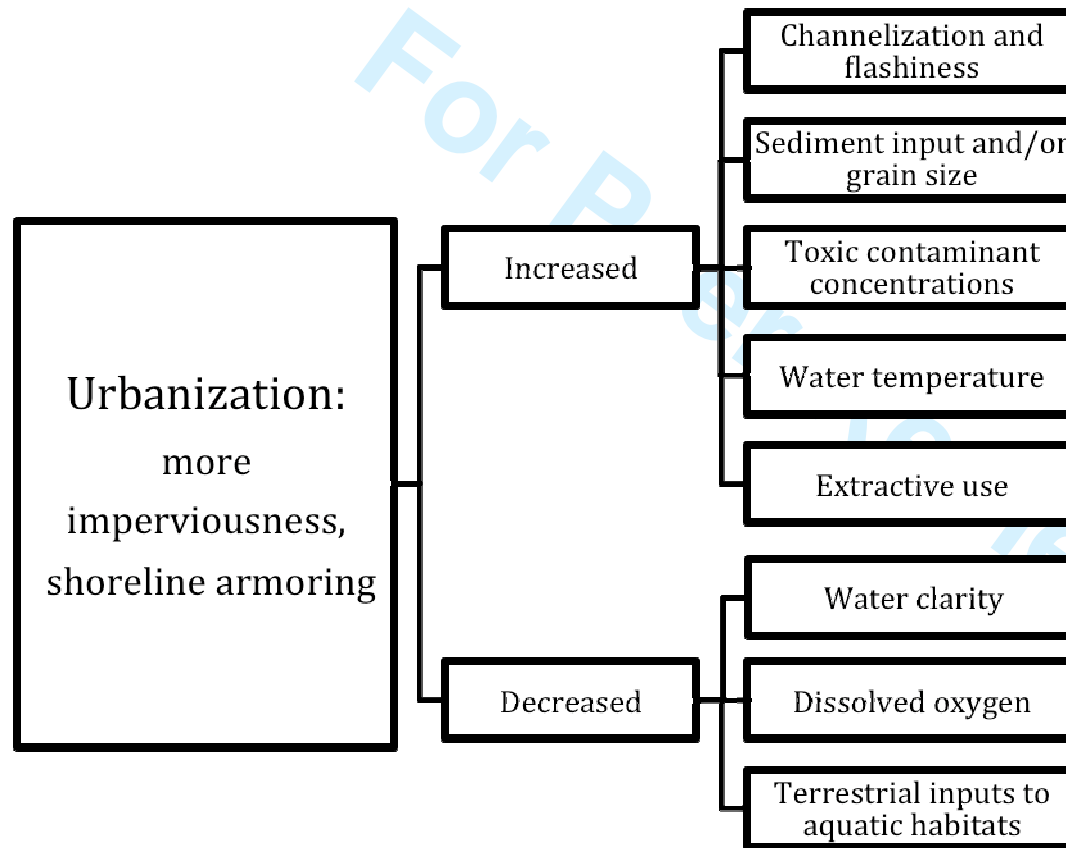662 Biodiversity Outlook. Montreal, 64 pages.
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710

711   **Tables**
712
713   Table 1. Examples of how urbanization, defined here as greater imperviousness and shoreline armoring, can modify
714   environmental processes, along with expected relationships between a variety of ecosystem properties. These example studies
715   suggest that the net effect of urbanization can lead to a broad diversity of ecosystem responses. For habitats, F = freshwater, M
716   = marine. See Supporting Information for full reference information.
717

Urbanization: more imperviousness, shoreline armoring	Increased	Channelization and flashiness
		Sediment input and/or grain size
		Toxic contaminant concentrations
		Water temperature
		Extractive use
	Decreased	Water clarity
		Dissolved oxygen
		Terrestrial inputs to aquatic habitats

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Ecosystem Property	Habitat	Specific Metric	Observed Response to Increased Urbanization	Reference
Biodiversity	F	Tolerant species	Positive	5, 14, 19
	F	Taxonomic richness	None or inconsistent	8
	F	Taxonomic richness	Negative	5, 14, 19
	F	Sensitive species	Negative	5, 14, 19
	M	Tolerant species	Positive	11
	M	Taxonomic richness	Positive	1
	M	Abundance	Inconsistent	16
	M	Biomass	None or inconsistent	2
	M	Taxonomic richness	None or inconsistent	9
	M	Density	None or inconsistent	12, 18
	M	Taxonomic richness	Negative	4, 7, 13, 16
	M	Evenness	Negative	6, 13
	M	Sensitive species	Negative	11
	M	Biomass	Negative	9
Decomposition	F	Decomposition rate	Positive	8
	F	Decomposition rate	Parabolic	5
	F	Leaf breakdown rate	None or inconsistent	19
Primary productivity	F	Chlorophyll a	Positive	17
	F	Gross primary productivity	None or inconsistent	8
	F	Algal biomass	None or inconsistent	19
	M	Gross primary productivity	Positive	3, 15
	M	Standing stock biomass	None or inconsistent	2
	M	Standing stock biomass	Negative	10

722 1. Bertasi *et al.* 2007, 2. Blake *et al.* 2014, 3. Bowen and Valiela 2001, 4. Bulleri and Chapman 2010, 5. Chadwick *et al.* 2008, 6.
723 Chapman and Underwood 2011, 7. Chapman 2003, 8. Clapcott *et al.* 2010, 9. Dugan *et al.* 2008, 10. Heerhartz *et al.* 2003, 11. Ingliss
724 and Kross 2000, 12. McKinley *et al.* 2011, 13. Morley *et al.* 2012, 14. Morse *et al.* 2003, 15. Savage *et al.* 2010, 16. Sobocinski *et al.*
725 2010, 17. Taylor *et al.* 2004, 18. Toft *et al.* 2007, 19. Walsh *et al.* 2005

726 **Table 2.** Description of data types and sampling methods. Superscripts indicate ecosystem properties likely to be associated with
727 specific environmental characteristics. F = freshwater, M = marine, D = decomposition, I = invertebrate biodiversity, P = net primary
728 productivity. All variables were collected from 12 study sites, except for freshwater biodiversity where we drew on 37 sites from the
729 Puget Sound Stream benthos database. See Supporting Information for full reference information.
730
731

Type of variable		Sampling Method	Year	N	Reference for Sampling Method
Biodiversity (of epibenthic macroinvertebrates)					
	Freshwater	Hess samples	2012-2013	3 site^{-1} year^{-1}	Hauer & Lamberti 2011; Wootton 2012; http://earth1.epa.gov/owow/monitoring/rbp/wp61pdf/rbp.pdf
	Marine	Sled tows	2012-2014	3 site^{-1} year^{-1}	Simenstad et al. 1991
Net primary productivity					
	Freshwater	Periphyton growth on tiles	2012-2013	10 site^{-1} year^{-1}	Wootton *2012*; Moore et al. 2007
	Marine	Algal growth on tiles	2012-2013	10 site^{-1} year^{-1}	Hixon & Brostoff 1996
Decomposition					
	Freshwater	10g litter bags *Acer* spp.	2012-2013	8 site^{-1} year^{-1}	Benfield 2006
	Marine	10g litter bags *Zostera marina*	2012-2013	8 site^{-1} year^{-1}	Nicastro et al. 2012; Bradford et al. 2002
Environmental characteristics					
Water temperature[FD, FP, MD, MP]		Temperature loggers deployed *in situ*	2012-2014	Hourly site^{-1} year^{-1}	Hauer & Lamberti 2011
	Stream flow[FD]	Float velocity method	2012-2013	3 times site^{-1}	Rantz et al. 1992

			year[-1]	
Stream canopy cover[FI, FP]	Densiometer	2012-2013	1 time site[-1] year^{-1}	Hauer & Lamberti 2011
Stream dimensions[FD]	Depth, wetted width	2012-2013	1 time site[-1] year^{-1}	Hauer & Lamberti 2011
Stream sediment size[FI]	% cobble, % gravel, % sand	2012	1 time site[-1]	Wolman 1954
Marine sediment size[MI]	% gravel, % sand, % fine	2013	1 time site[-1]	Dethier and Schoch 2006
Nutrients[FP,MP]	NO_3^-, NH_4^+, NO_2^-, SiO_4^{4-}, PO_4^{3-} (μg/L)	2013	1 time site[-1]	http://www.ocean.washington.edu/file/Sampling+Procedures; See Supporting Information for details
Marine salinity[MI]	Refractometer	2012-2014	3-5 times site[-1] year^{-1}	Pilson 2012
Wave exposure[MD, MI]	Spatial analysis of wind speed and velocity weighted fetch	1980-2010	30-year mean	See Supporting Information for details

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734   **Figures**
735
736   Figure 1. Map of watershed locations for this study, along with a principal components
737   analysis of watershed pairs used to define the urban gradient. Larger values of PC1 and
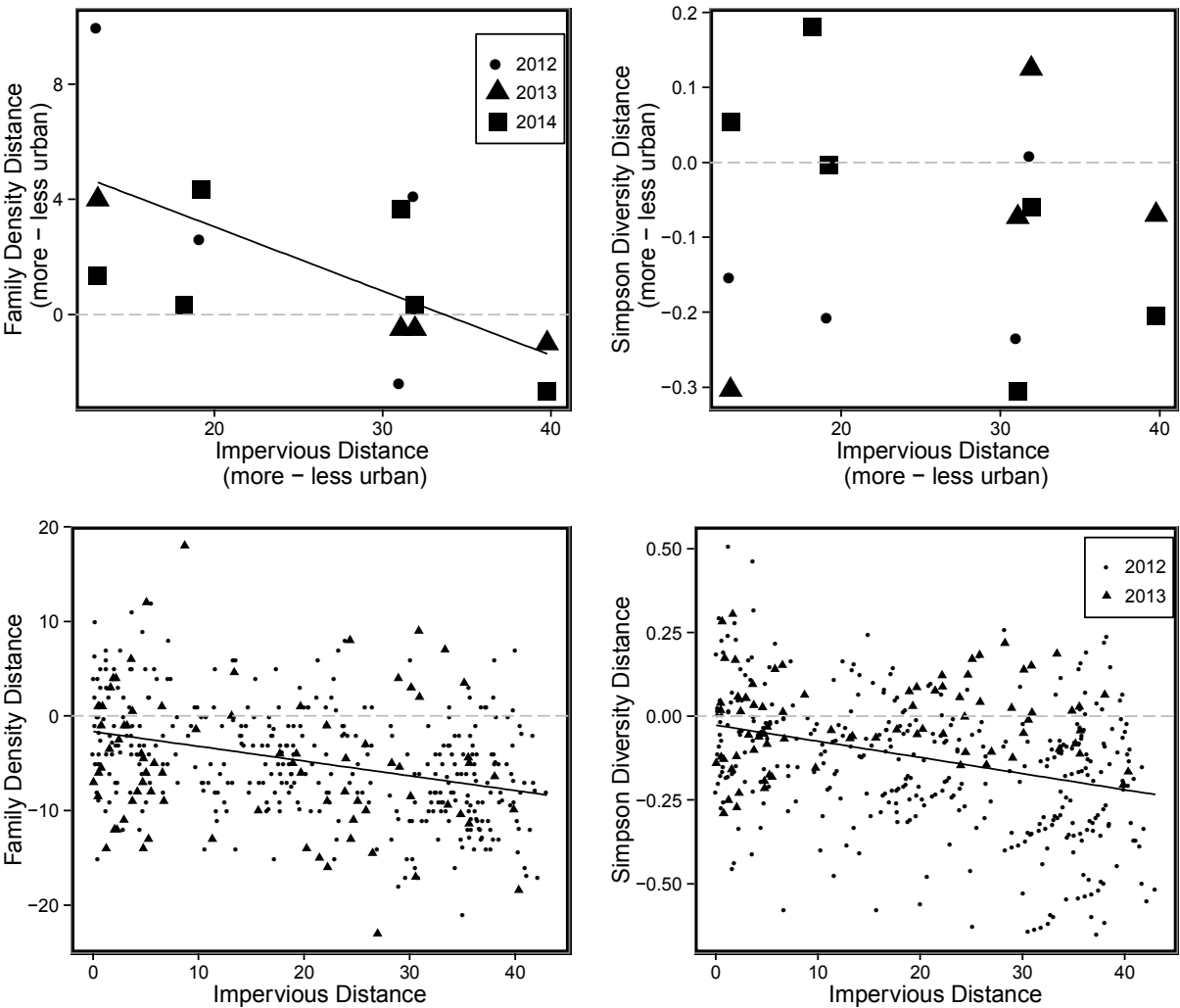738   PC2 indicate increasing urbanization.
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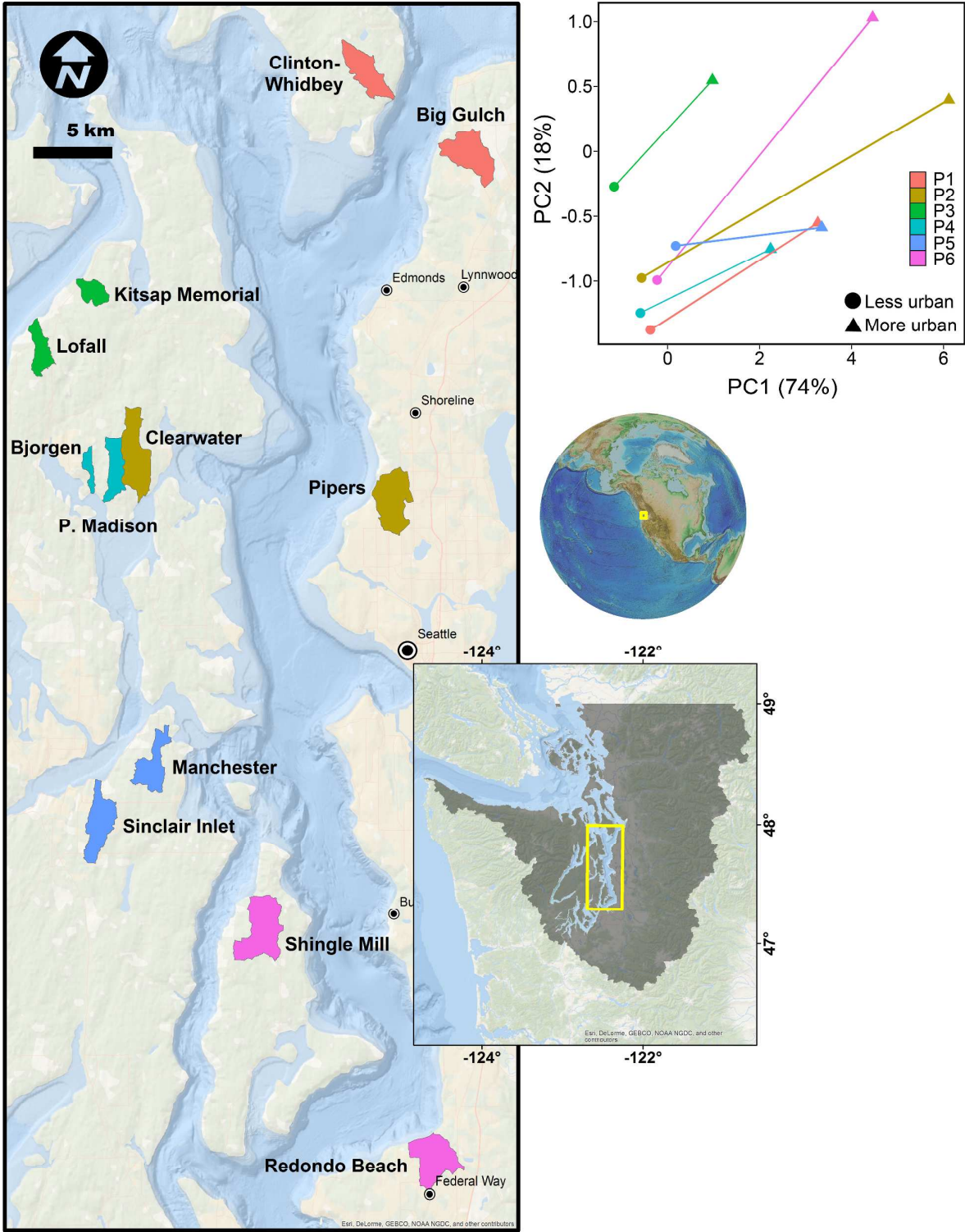
741   Figure 2. Associations between impervious distance and disparity between more and less urbanized watersheds in two measures of
742   invertebrate diversity (left, Family Density; right, Simpson Diversity) in marine (top row) and freshwater (bottom row) habitats. Solid
743   regression lines indicate statistically significant associations, whereas the dashed lines represent zero difference in the diversity indices
744   between more and less urbanized watersheds.

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746

747 Figure 3. Associations between impervious distance and disparity between more and less urbanized watersheds in two ecosystem
748 functions (left, Net Primary Productivity; right, Decomposition) in marine (top row) and freshwater (bottom row) habitats. No
749 regressions were statistically significant; the dashed lines represent zero difference in the ecosystem properties between more and less
750 urbanized watersheds.

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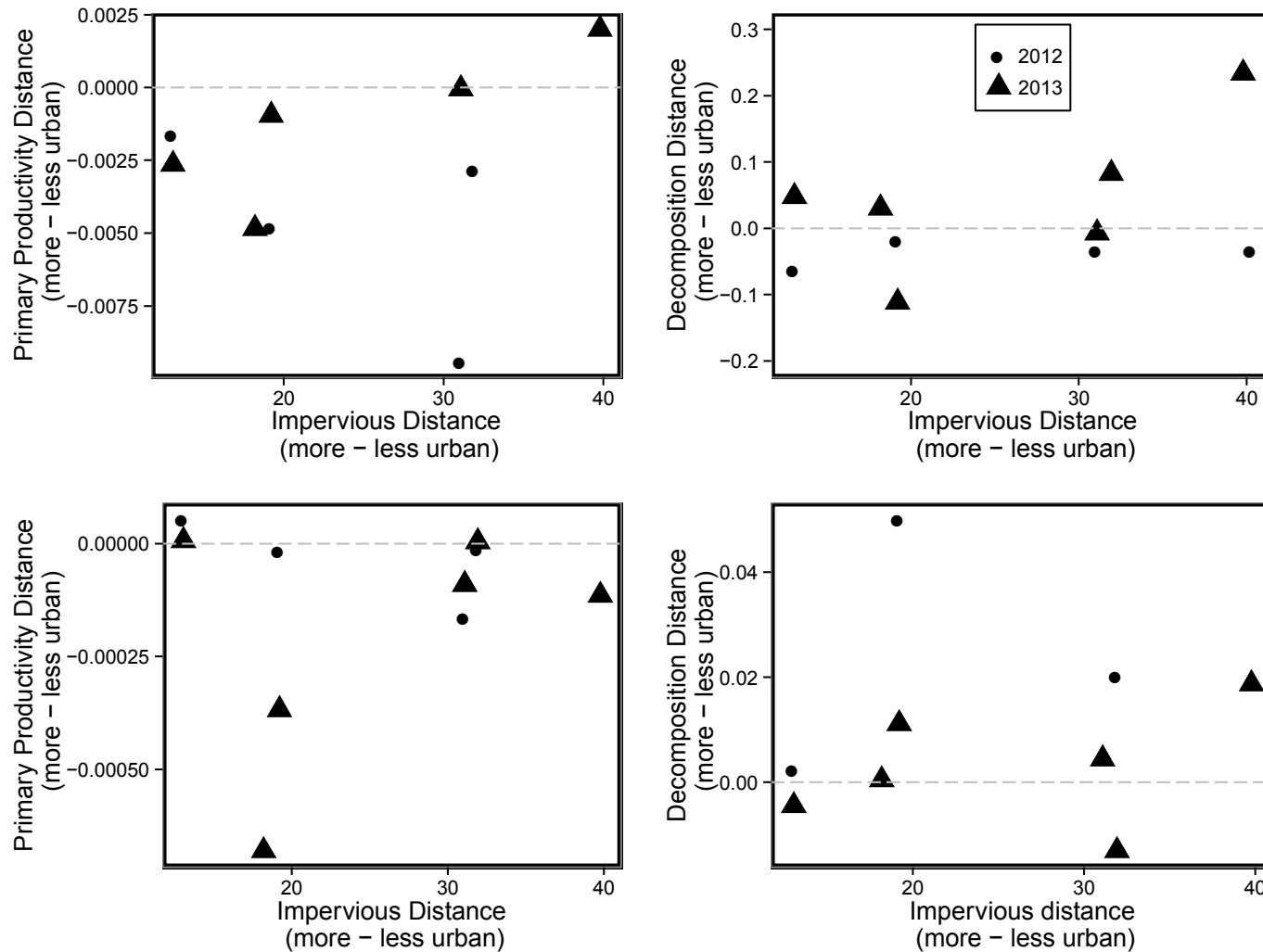
753   Figure 4. Mean effect sizes (with 95% CI) for relationships between biodiversity distance (top:
754   family density; bottom: Simpson diversity) and impervious distance in freshwater and marine
755   habitats. Effect sizes related to two ecosystem functions (net primary productivity and
756   decomposition) also did not differ between habitat types.
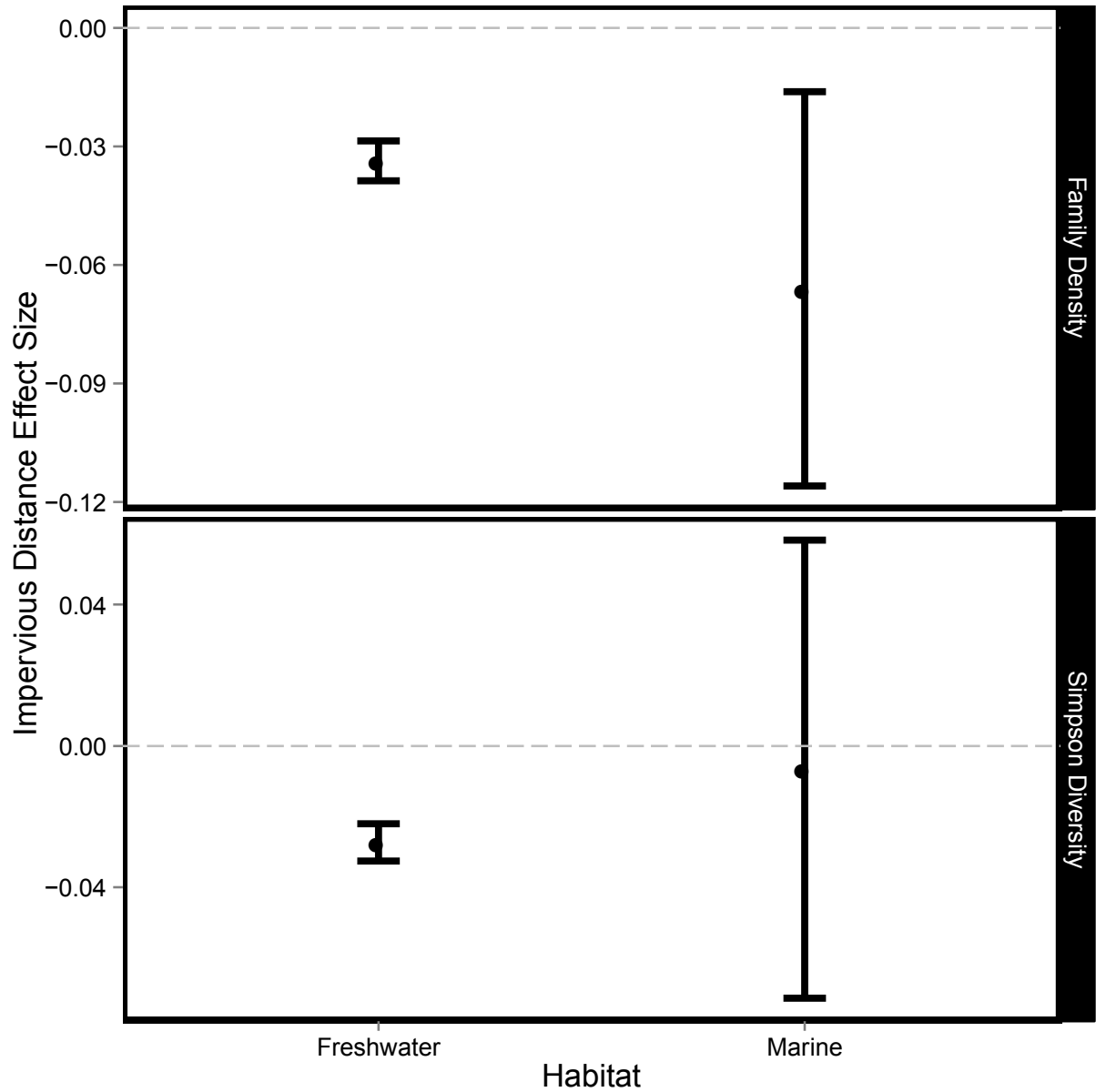
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1   **Supporting Information**
2
3   *Characterizing variability in urbanization and ecosystem properties: defining the urban gradient*

4   Table S1. (a) PCA Results for urban gradient analysis.
5

PC	Eigenvalues	%Variation	Cum.%Variation
1	2.96	74.0	74.0
2	0.723	18.1	92.1
3	0.293	7.3	99.4
4	2.24E-2	0.6	100.0

6
7   (b) Eigenvectors (coefficients in the linear combinations of variables making up PC's).

Variable	PC1	PC2	PC3	PC4
Imperviousness (%)	0.555	-0.230	-0.369	0.710
Road density	0.512	-0.142	0.847	-0.005
Armor (%)	0.352	0.934	-0.056	-0.003
Developed land (%)	0.554	-0.234	-0.378	-0.704

8
9
10   *Other environmental characteristics*
11   In addition to quantifying elements of ecosystem structure (epibenthic macroinvertebrate
12   diversity) and function (net primary productivity and decomposition rates) in freshwater and
13   marine habitats at each of the study watersheds, we measured several other environmental
14   characteristics that may influence these ecosystem properties. Specifically, in both freshwater
15   and marine habitats, we quantified water temperature hourly using *in situ* loggers during all
16   sampling periods. In addition, we determined freshwater and marine water nutrient
17   concentrations (NO_3, NO_2, NH_4, PO_4, $SiOH_4$) by collecting samples in July 2013 (n = 3
18   freshwater and 3 marine samples site^{-1}).
19   In freshwater habitats, at the same time we were sampling ecosystem structural and
20   functional properties, we estimated flow velocity using the float velocity method; canopy cover
21   using a densiometer; and, stream dimensions (bankfull width, wetted width, depth) and sediment
22   size following the protocols described by Hauer and Lamberti (2006) and others (see Table 2).
23   In marine habitats, we used a refractometer to estimate salinity during each site visit. We
24   collected sediments in August 2013 to quantify grain size distributions following the methods of
25   Dethier and Schoch (2006).
26   In order to characterize the relative exposure at each of our study sites, we used the
27   Waves (v. 2012) tool (Rohweder et al. 2012) in ArcGIS to calculate a wind speed and direction
28   weighted fetch distance for Puget Sound. We ran our model over a spatial domain spanning
29   47.0° to 49.5°N latitude and -122.2° to -124.6°W longitude, with a spatial grain or resolution of
30   50 m. The tool used two types of data: shoreline and wind. For the Canadian and the US portions
31   of the shoreline (converted from vector to 50 m grid), we used NASA's world surface water
32   body data (downloaded from http://gis.ess.washington.edu/data/vector/worldshore/index.html)
33   and USGS digital line graph (DLG), respectively. For the wind data, we used "normal" hourly
34   wind direction and velocity for the Sea-Tac International Airport weather station (Arguez et al.
35   2010), based on data from 1980-2010. We used this wind station because it was central to all of

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36 our sites and had a complete data record from 1980 – 2010. We used the SPM-Restricted option
37 in the Waves tool to generate wind direction and speed weighted fetch distances for all of the 50
38 m grid cells in the study area. Finally, we overlaid the point locations for each of our marine
39 study sites with the resulting weighted fetch distance grid and captured the relative wave
40 exposure value for each site.
41   These data were used to estimate an average for each of the environmental characteristics
42 at all of our sites during the study periods of each year.
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Table S2. Study site characteristics.

Site name	Pair	Basin area (ha)	Imperv	Roads (m/ha)	Armor (%)	Devel (%)	PC1	PC2	Eelgrass
Clinton-Whidbey	P1	537	1.7	28.9	77	2.8	-0.37	1.38	patchy
Big Gulch *	P1	671	33.7	44.6	100	57.9	3.27	0.55	patchy
Clearwater Casino	P2	743	2.4	20.9	61	4.5	-0.56	0.98	thick
Pipers Creek *	P2	730	42.2	157.2	100	83.1	6.12	-0.40	patchy
Kitsap Memorial	P3	234	1.3	9.2	29	2.4	-1.16	0.27	absent
Lofall *	P3	307	14.4	48.1	28	34.0	0.98	-0.55	patchy
Port Madison	P4	368	2.2	15.5	70	3.7	-0.59	1.24	absent
Bjorgen Creek *	P4	128	21.4	54.9	91	41.2	2.24	0.75	absent
Manchester	P5	481	7.2	35.7	62	13.7	0.18	0.73	patchy
Sinclair Inlet *	P5	587	25.4	78.4	100	58.4	3.35	0.59	patchy
Shingle Mill	P6	842	4.1	33.1	65	5.1	-0.23	0.99	thick
Redondo Beach *	P6	684	35.2	108.2	58	78.0	4.46	-1.03	patchy

* more urbanized of given site pair

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Table S3. Marine invertebrate taxa included in the diversity analyses.

Marine taxa:

	Class	**Order**	**Family**
Crabs	Malacostraca	Decapoda	Cancridae
	Malacostraca	Decapoda	Cheiragonidae
	Malacostraca	Decapoda	Epialtidae
	Malacostraca	Decapoda	Grapsidae
	Malacostraca	Decapoda	Majidae
	Malacostraca	Decapoda	Paguridae
	Malacostraca	Decapoda	Pinnotheridae
	Malacostraca	Decapoda	Porcellanidae
Shrimps	Malacostraca	Decapoda	Crangonidae
	Malacostraca	Decapoda	Hippolytidae
	Malacostraca	Decapoda	Pandalidae
Isopods	Malacostraca	Isopoda	Cirolanidae
	Malacostraca	Isopoda	Idoteidae
	Malacostraca	Isopoda	Munnidae
	Malacostraca	Isopoda	Unidentified parasitic isopod
	Malacostraca	Isopoda	Sphaeromatidae
Amphipods	Malacostraca	Amphipoda	Caprellidae
	Malacostraca	Amphipoda	Gammaridae
Other Arthropods	Malacostraca	Cumacea	Cumacean_unid
	Malacostraca	Cumacea	Diastylidae
	Malacostraca	Cumacea	Lampropidae
	Malacostraca	Leptostraca	Nebaliidae
	Malacostraca	Mysida	Unidentified mysid
	Malacostraca	Tanaidacea	Unidentified tanaid
	Maxillopoda	Arguloida	Argulidae
	Pycnogonida	Pantopoda	Unidentified pantopod
Gastropods	Gastropoda	Caenogastropoda	Assimineidae
	Gastropoda	Caenogastropoda	Batillariidae
	Gastropoda	Caenogastropoda	Calyptraeidae

	Gastropoda	Caenogastropoda	Cerithiidae
	Gastropoda	Neogastropoda	Columbellidae
	Gastropoda	Neogastropoda	Muricidae
	Gastropoda	Neogastropoda	Nassariidae
	Gastropoda	Neogastropoda	Olividae
	Gastropoda	Littorinimorpha	Littorinidae
	Gastropoda	Littorinimorpha	Rissoellidae
	Gastropoda	Littorinimorpha	Rissoidae
	Gastropoda	Vetigastropoda	Calliostomatidae
	Gastropoda	Vetigastropoda	Trochidae
	Gastropoda	Heterobranchia	Pyramidellidae
	Gastropoda	Heterobranchia	Unidentified pteropod
	Gastropoda	Cephalaspidea	Haminoeidae
	Gastropoda	Sacoglossa	Hermaeidae
	Gastropoda	Aeolidida	Facelinidae
	Gastropoda	Doridacea	Dorididae
Other Molluscs	Neoloricata	Chitonida	Ischnochitonidae
	Neoloricata	Chitonida	Mopaliidae
Echinoderms	Asteroidea	--	Unidentified asteroid
	Echinoidea	Clypeasteroida	Dendrasteridae
	Echinoidea	Echinoida	Strongylocentrotidae
	Holothuroidea	Dendrochirotida	Unidentified holothurid
	Ophiuroidea	Ophiurida	Unidentified ophiurid
Other Taxa	Turbellaria	--	Unidentified platyhelminthid
	Anthozoa	Actiniaria	Actiniidae

7

Table S4. Freshwater invertebrate taxa and relative proportion (%) across all samples included in the diversity analyses

Aeshnidae (0.031)	Dolichopodidae (0.040)	Lebertiidae (1.560)	Pleuroceridae (0.292)
Ameletidae (0.541)	Dryopidae (0.004)	Lepidostomatidae (1.777)	Polycentropodidae (0.089)
Ancylidae (0.479)	Dytiscidae (0.616)	Leptoceridae (0.102)	Protziidae (0.323)
Anisitsiellidae (0.009)	Elmidae (4.365)	Leptohyphidae (0.049)	Psephenidae (0.018)
Anisogammaridae (0.093)	Empididae (3.328)	Leptophlebiidae (2.242)	Psychodidae (1.068)
Apataniidae (0.301)	Enchytraeidae (1.604)	Leuctridae (1.072)	Psychomyiidae (0.075)
Arcidae (0.009)	Ephemerellidae (2.162)	Libellulidae (0.004)	Pteronarcyidae (0.643)
Arrenuridae (0.071)	Ephemeridae (0.004)	Limnephilidae (1.733)	Ptychopteridae (0.151)
Asellidae (0.487)	Ephydridae (0.222)	Limnesiidae (0.062)	Pyralidae (0.004)
Astacidae (0.408)	Erpobdellidae (0.137)	Lumbricidae (0.004)	Rhyacophilidae (4.006)
Athericidae (0.053)	Feltriidae (0.004)	Lumbriculidae (1.671)	Sciomyzidae (0.053)
Athienemanniidae (0.022)	Gammaridae (0.049)	Lymnaeidae (0.177)	Scirtidae (0.004)
Aturidae (0.022)	Gerridae (0.022)	Margaritiferidae (0.062)	Sialidae (0.146)
Axonopsidae (0.004)	Glossiphoniidae (0.080)	Mideopsidae (0.253)	Simuliidae (4.431)
Baetidae (4.830)	Glossosomatidae (3.474)	Muscidae (0.027)	Sperchonidae (1.236)
Blephariceridae (0.071)	Goeridae (0.031)	Mycetophilidae (0.013)	Sphaeriidae (1.546)
Brachycentridae (1.427)	Gomphidae (0.053)	Naididae (1.099)	Sphaeromatidae (0.031)
Caenidae (0.035)	Gyrinidae (0.004)	Nautarachnidae (0.035)	Stratiomyidae (0.022)
Calamoceratidae (0.031)	Haliplidae (0.093)	Nemouridae (4.453)	Syllidae (0.523)
Capniidae (0.425)	Haplotaxidae (0.018)	Neoacaridae (0.004)	Tabanidae (0.053)
Carabidae (0.009)	Helicopsychidae (0.018)	Notonectidae (0.004)	Taeniopterygidae (0.044)
Ceratopogonidae (2.477)	Helophoridae (0.004)	Odontoceridae (0.018)	Tanyderidae (0.009)
Chaoboridae (0.004)	Heptageniidae (3.438)	Oxidae (0.053)	Tetrastemmatidae (0.018)
Chironomidae (5.078)	Hirudinidae (0.004)	Pelecorhynchidae (1.046)	Thaumaleidae (0.191)
Chloroperlidae (3.930)	Hyalellidae (0.097)	Peltoperlidae (0.341)	Thyasidae (0.013)
Coenagrionidae (0.097)	Hydrachnidae (0.004)	Perlidae (2.229)	Tipulidae (4.063)
Corbiculidae (0.027)	Hydraenidae (0.155)	Perlodidae (3.248)	Torrenticolidae (0.660)
Cordulegastridae (0.009)	Hydridae (0.204)	Philopotamidae (1.263)	Tubificidae (0.182)
Corixidae (0.075)	Hydrobiidae (0.261)	Phryganeidae (0.004)	Uenoidae (1.382)
Corophiidae (0.049)	Hydrodromidae (0.004)	Physidae (0.315)	Unionicolidae (0.027)

Crambidae (0.044)	Hydrophilidae (0.230)	Pionidae (0.022)	Unionidae (0.009)
Crangonyctidae (1.728)	Hydropsychidae (4.143)	Piscicolidae (0.044)	Valvatidae (0.022)
Culicidae (0.009)	Hydroptilidae (0.580)	Pisidiidae (0.962)	
Deuterophlebiidae (0.004)	Hydryphantidae (0.031)	Planariidae (0.846)	
Dixidae (1.874)	Hygrobatidae (0.824)	Planorbidae (0.793)	

1   Figure S1. Results from paired t tests examining differences between more and less urban sites
2   within a pair in each of 8 ecosystem properties. Figures represent 95% confidence intervals, such
3   that negative values with CIs that do not overlap zero suggest a greater value of the ecosystem
4   property in less urban sites (marine primary productivity, stream family density, stream
5   Simpson's diversity) and vice versa (none).
6
7   For more than half of the ecosystem properties we tracked, more urbanized watersheds were no
8   different than less urbanized watersheds (only 3 of 8 paired t-tests were significant). In marine
9   habitats invertebrate family density tended to be higher, and Simpson diversity tended to be
10 lower, in more urbanized than less urbanized watersheds, though neither of these differences was
11 significant. In contrast, marine net primary productivity was significantly lower in more
12 urbanized than less urbanized watersheds, but there was no significant difference in marine
13 decomposition between more and less urbanized watersheds. In freshwater habitats, more
14 urbanized watersheds were characterized by significantly lower invertebrate family density and
15 Simpson diversity than less urbanized watersheds. Neither of the ecosystem functions we
16 measured in freshwater habitats differed between more and less urbanized watersheds.
17

18
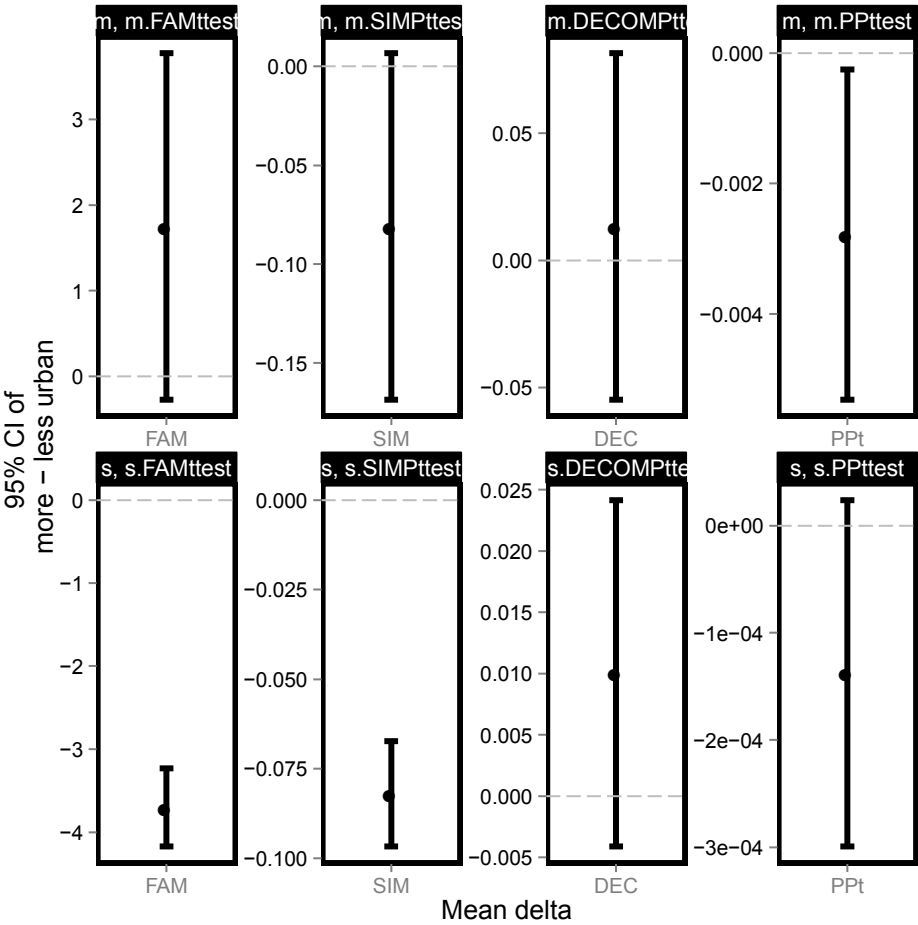
Figure S2. Environmental characteristics likely to be associated with biodiversity (F: summer stream water temperature, stream flow, stream dimensions; M: summer marine water temperature, exposure), net primary productivity (F: summer stream water temperature, stream canopy cover, stream nutrient concentrations; M: sum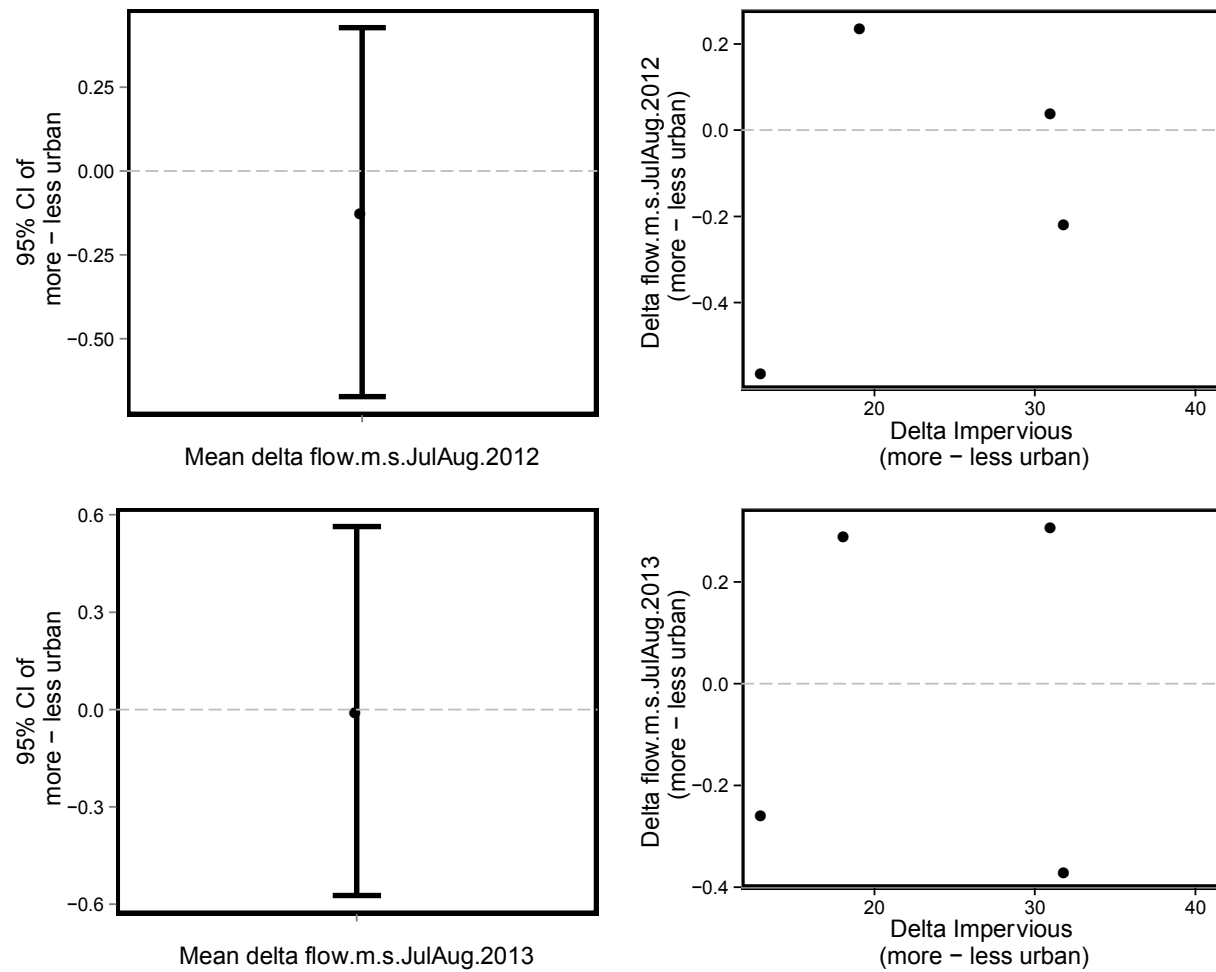mer marine water temperature, marine nutrient concentrations), and decomposition (F: fall stream water temperature, stream flow, stream dimensions; M: fall marine water temperature, exposure) did not differ significantly between more and less urban watershed pairs or change significantly with increasing impervious distance. The only exception was for stream PO4 concentrations, which were significantly higher in less urban than more urban watersheds. (a) Summer stream water temperature , (b) Fall stream water temperature, (c) Stream flow, (d) Stream dimensions, (e) Stream canopy cover, (f) Stream nutrient concentrations, (g) Summer marine water temperature, (h) Marine exposure, (i) Marine nutrient concentrations.

(a) Summer stream water temperature

(b) Fall stream water temperature

(c) Stream flow

(d) Stream dimensions

(e) Stream canopy cover

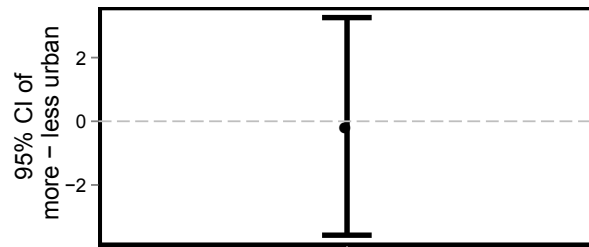Mean delta mean.prop.canopy.cover.2012

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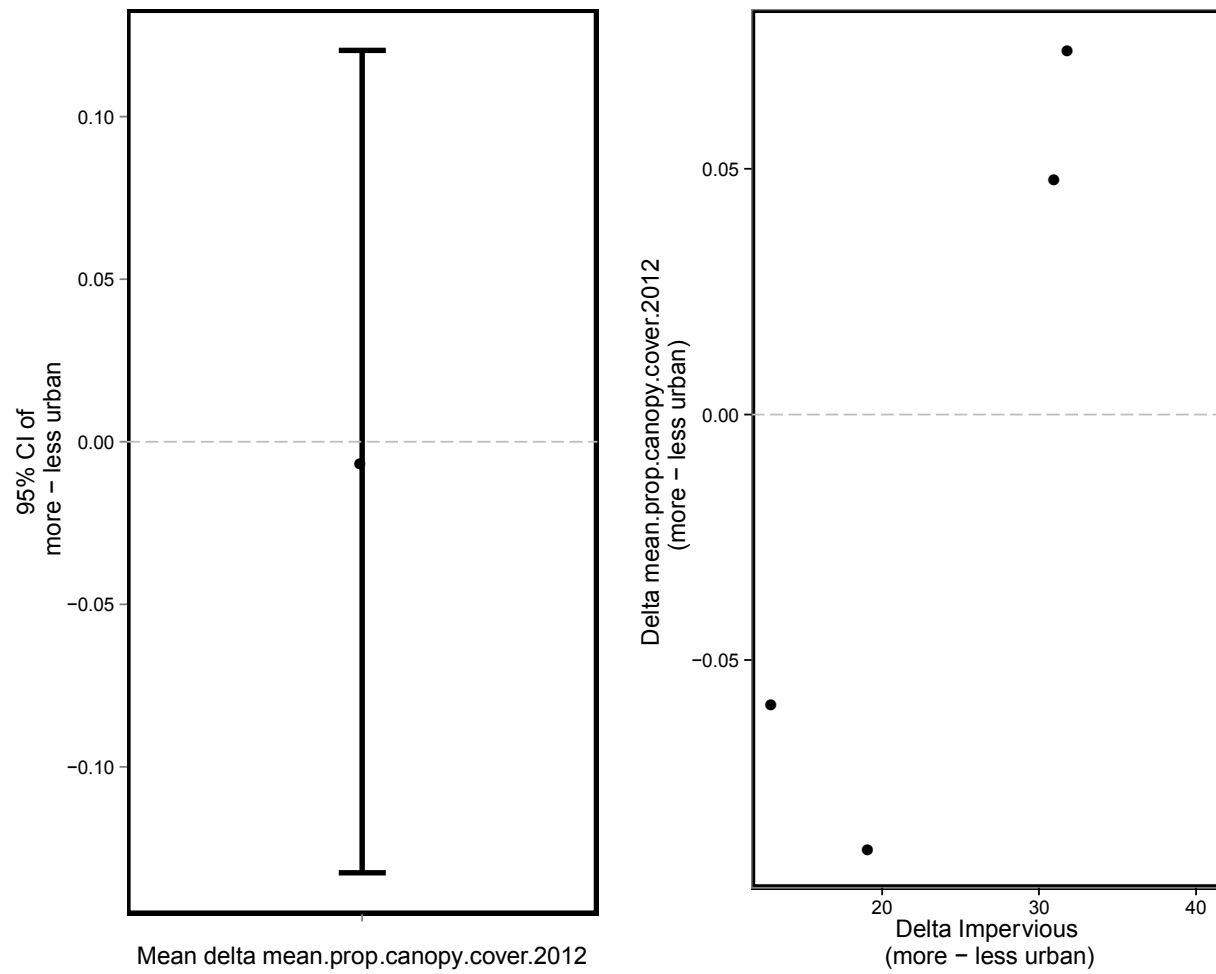
(f) Stream nutrient concentrations
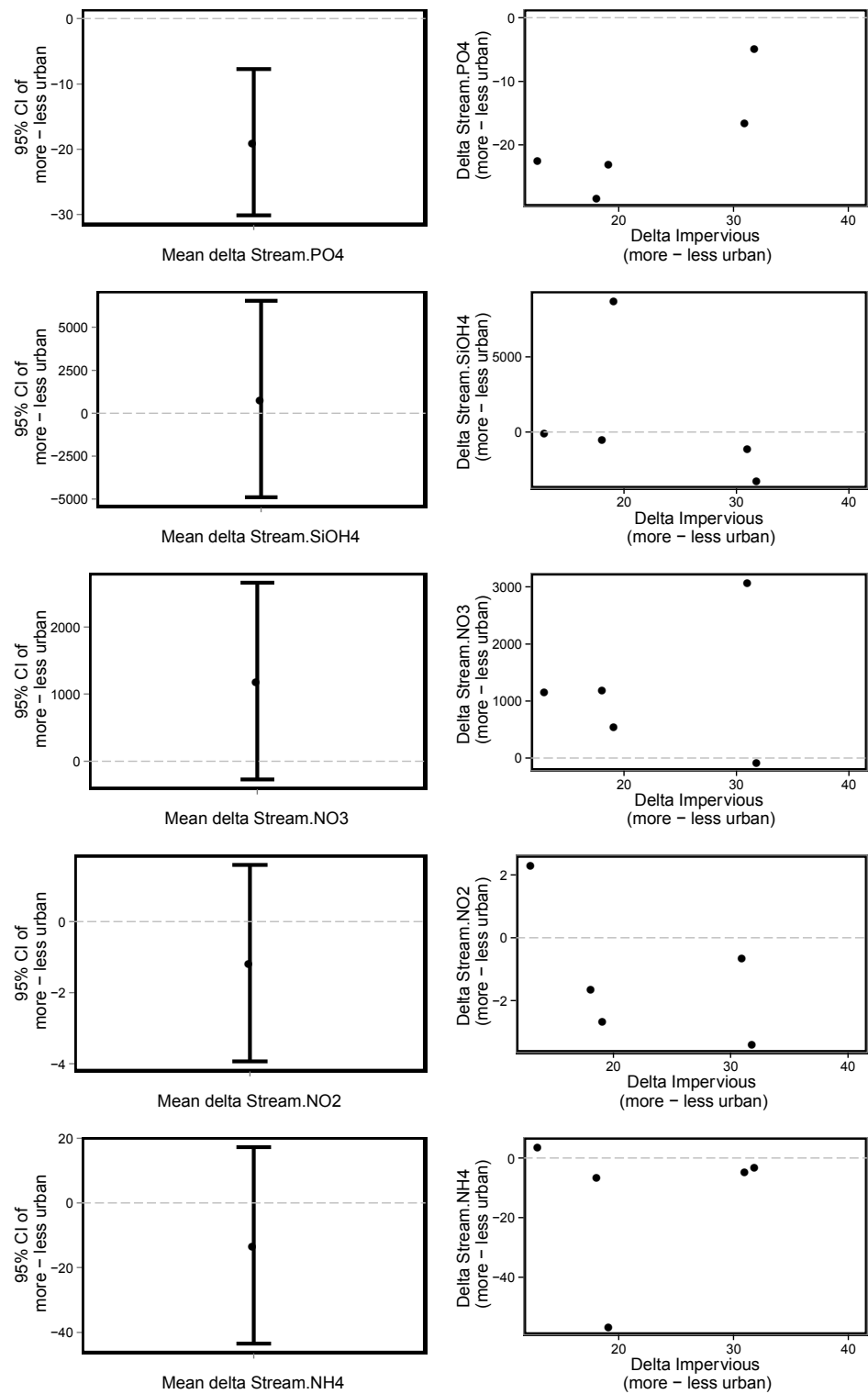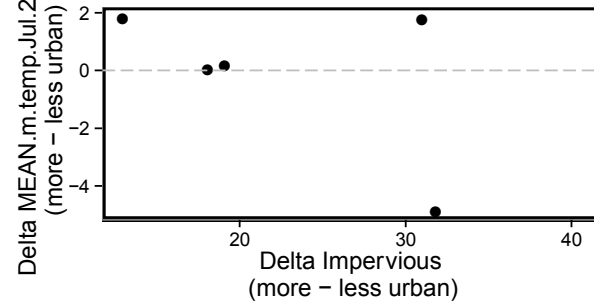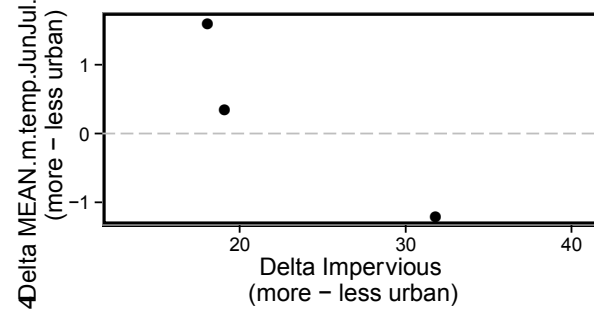
(g) Summer marine water temperature
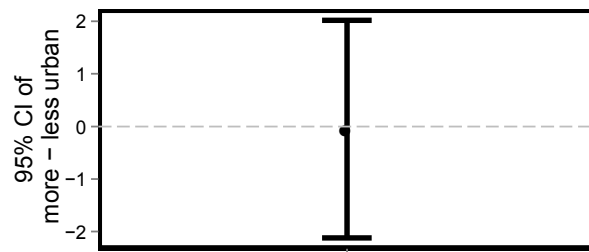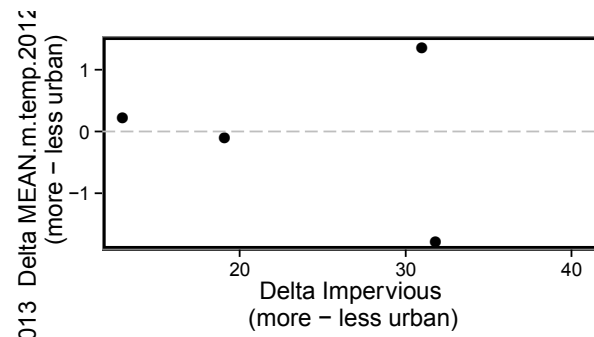

Mean delta MEAN.m.temp.2012
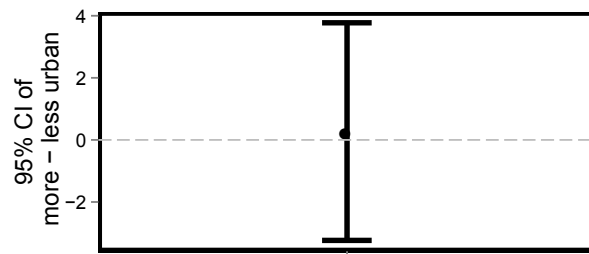
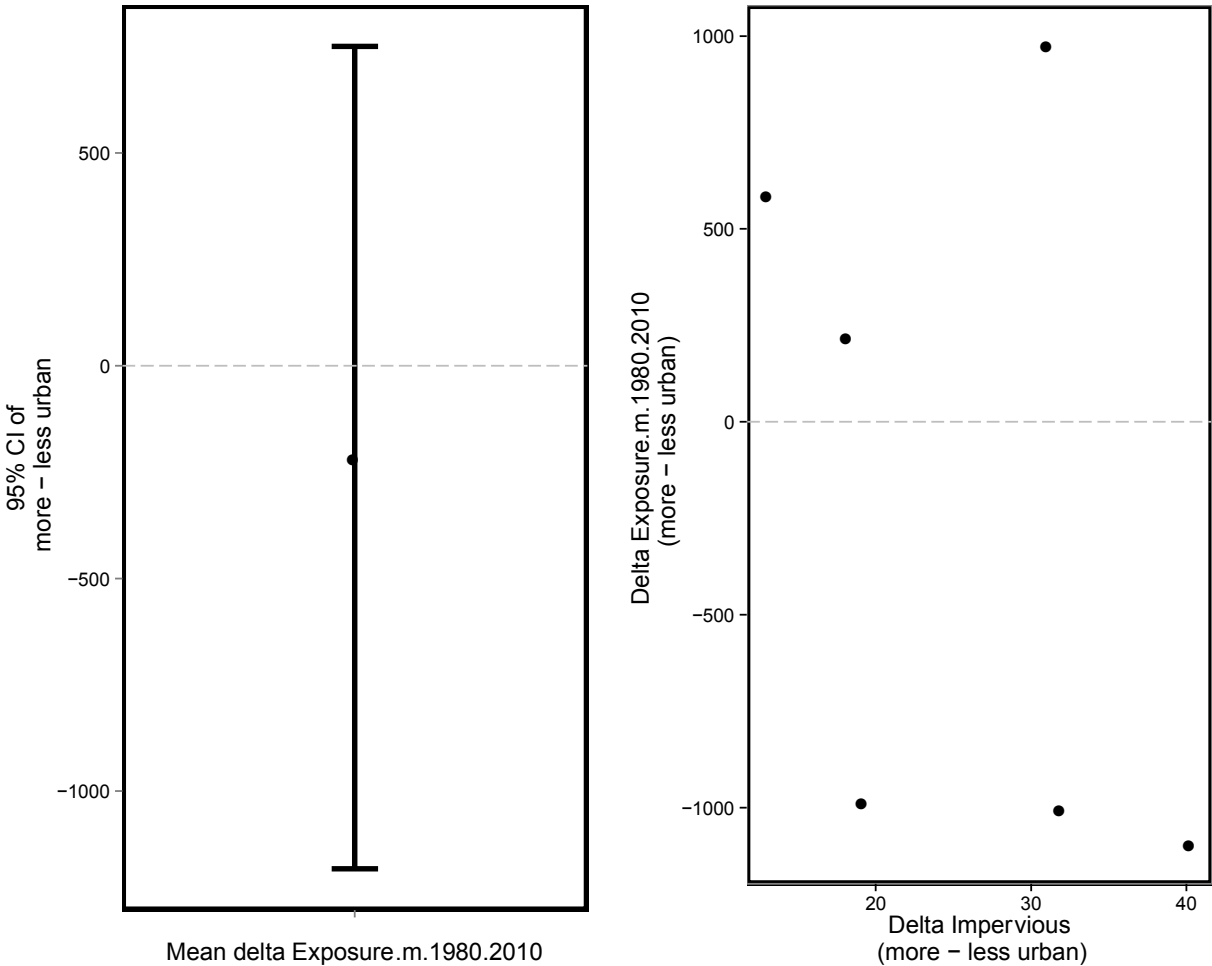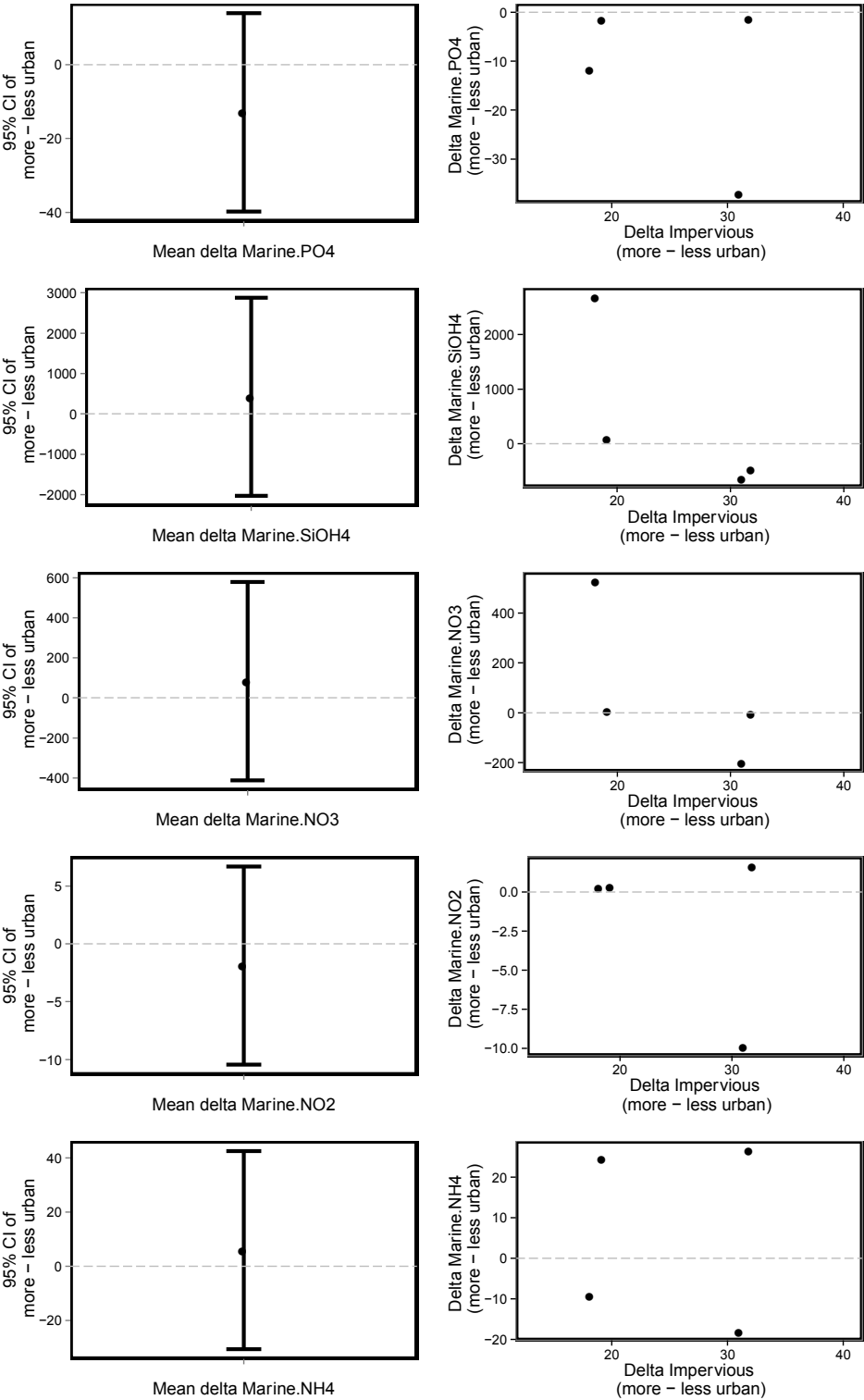Mean delta MEAN.m.temp.JunJul.2013

Mean delta MEAN.m.temp.Jul.2014

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(h) Marine exposure

1   (i) Marine nutrient concentrations

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